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MENDELISM AND INTERSPECIFIC HYBRIDS

THE complications of modern Mendelism have greatly increased the difficulty of discussing the practical applications of heredity. The word Mendelism itself has two essentially different meanings that are being used indiscriminately. A particular form of alternative inheritance is called Mendelism and the same name is applied to a general theory of heredity. It is true that the Mendelian theory was suggested by the Mendelian form of inheritance, but the facts are also capable of other interpretations. Many of the proposed applications of Mendelism to breeding and eugenics are in reality only inferences from the theory and are not in real accord with the facts on which they are supposed to be based.

An example of such a discrepancy may be found in the AMERICAN NATURALIST for July, 1912, in a paper entitled: "Evidence of Alternative Inheritance in the F_2 Generation from Crosses of *Bos indicus* on *Bos taurus*." Though readers are evidently expected to believe that the hybrids are showing a typical Mendelian inheritance of the contrasted parental characters, the facts stated in the paper show that the behavior of the hybrids is not in accord with the Mendelian theory of heredity. Alternative inheritance is manifested in these bovine hybrids, but it is not the Mendelian form of alternative inheritance, with the contrasted parental characters behaving as independent units combined by the laws of chance. Instead of showing a Mendelian freedom of combination of the contrasted characters, these hybrids afford a much better illustration of a different principle of heredity, the coherence of characters derived from the same parental stock.

As the paper by Dr. Nabours seems to represent the only attempt that has been made to give a scientific account of a unique series of hybrids, it would be very undesirable to have the general conclusion regarding the application of Mendelism accepted without challenge. In addition to the scientific questions involved, the importance of finding the best way of securing a full utilization of the tick-resistant Brahma cattle in Texas will appeal to all who have had the pleasure of seeing Mr. Borden's imported animals and their hybrid offspring. But practical recommendations are hardly in order until the facts are better understood. To view these hybrids as a typical case of Mendelism is to overlook some of the distinctions which need to be recognized before correct applications can be expected.

ALTERNATIVE INHERITANCE

It seems to be taken for granted by Dr. Nabours, as by many other recent writers, that all forms of alternative inheritance represent the so-called Mendelian principle of heredity, that is, the alternative transmission of unit-characters in pure germ-cells. In reality the facts of alternative inheritance extend far beyond the field of Mendelism into regions where the Mendelian conception of alternative transmission can not be applied.[1]

The old assumption regarding hybrids and mixed races was that they represented intermediate combinations or averages between the contrasted characters of the parental stocks. A generation ago belief in "the swamping effects of intercrossing" was even more general among biologists than acceptance of Mendelism is now. But we have learned that the "swamping effects" were largely imaginary. The scientific world has its history of easily forgotten fads, no less than the world of politics or fashion.

The usual result of crossing is not the formation of an intermediate average, but the reappearance of the parental characters in the later generations of the hybrids, if not in the first. Recognition of the principle of alternative inheritance is having a revolutionary effect upon the science of heredity. The facts of Mendelism are of special interest because they represent extreme cases of alternative inheritance, but the interest is in no way dependent upon the Mendelian theory of heredity. Indeed, the theory often interferes with appreciation of the facts.

MENDELISM A THEORY OF ALTERNATIVE TRANSMISSION

Mendelism, as a theory of heredity, is an assumption that alternative inheritance is due to alternative transmission of independent particles or "units," which are supposed to represent the characters in the protoplasm at the time when the germ-cells are formed. If sufficient magnification could be applied, so that the structure of the protoplasm in the germ-cells could be fully shown, believers in the Mendelian theory would expect to find separate "gens" or discrete particles of some sort to represent the various characters of the adult animals or plants. The gens that represent the characters of different parents are supposed to remain entirely distinct and to find their ways into different germ-cells. Each germ-cell of a hybrid is supposed to receive only a single set of these hypothetical character-units or gens, representing the contrasted characters of the parents, and the sets are supposed to be made up by chance assortment. Thus the different germ-cells produced by a hybrid are supposed to represent all the combinations of the contrasted parental characters that are theoretically possible under the laws of chance.

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[1] Cook, O. F., "Dimorphic Leaves of Cotton and Allied Plants in Relation to Heredity," Bulletin 221, Bureau of Plant Industry, U. S. Department of Agriculture, pp. 36–50.

The theory of Mendelism has greatly stimulated the study of cytology, in the hope of finding the supposed character-germs as actual, visible particles in the protoplasm. Some writers have argued that the chromosomes or chromomeres represent the characters, or at least the contrasted Mendelian characters, and have attempted to trace a definite relation between the behavior of the chromosomes and the inheritance of the characters. Other writers do not indulge in such speculations, but believe in alternative transmission for mathematical reasons. Typical cases of Mendelism are relied upon as affording sufficient proof of the theory of alternative transmission. The Mendelian theory accords with the numerical facts of Mendelism, but this is not a sufficient proof of its correctness, for it is not the only interpretation that the facts will admit. Elaborate Mendelian computations create in the casual reader an impression of mathematical certainty, but the same computations could be made under other theories of alternative inheritance.

Alternative Inheritance and Normal Diversity

The facts of alternative inheritance are not at all confined to cases where the characters show the exact numerical proportions typical of Mendelism. Alternative inheritance is a general law that applies even in the vast and highly diversified groups of interbreeding individuals that constitute natural species. The typical Mendelian cases usually appear as results of previous artificial breeding of pure strains.[2]

The normal diversity (heterism) everywhere manifested among the members of natural species is a result of alternative inheritance of contrasted parental characters, no less than the typical cases of Mendelism. If inheritance were not alternative, heterism would not be maintained. Each species or separate group of interbreeding individuals would gradually decline into a general uniform average. Under conditions of normal interbreeding among the representatives of different lines of descent there is no such tendency to uniformity. The offspring of the same parents differ normally among themselves in the same ways that the parents and ancestors have differed. Though each individual can bring into expression only one set of differences, other ancestral characters are likely to reappear in later generations. It is only by special methods of breeding in single or narrow lines of descent that conditions of uniform heredity can be established.

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[2] Cook, O. F., "Pure Strains as Artifacts of Breeding," The American Naturalist, 43: 241, April, 1909.

ALTERNATIVE EXPRESSION INSTEAD OF ALTERNATIVE TRANSMISSION

That characters are transmitted without being brought into expression is one of the best known facts of heredity, for which the theory of Mendelism makes no adequate provision. The idea of alternative expression of characters accommodates the numerical data of Mendelism as well as the idea of alternative transmission, and is in far better accord with other facts of variation. Diversity in natural species, and reversions that arise in select varieties and in hybrid stocks, afford adequate evidence for holding that alternative inheritance is due, not to alternative transmission of characters, but to alternative expression. When the facts of alternative expression are taken into account the theory of alternative transmission becomes unnecessary.[3]

COHERENCE OF CHARACTERS IN INTERSPECIFIC HYBRIDS

The contrasted characters of interspecific hybrids do not behave as independent Mendelian units, but tend to remain more or less united with others derived from the same parental stock. This coherence of expression often interferes with the formation of the combinations of characters according to the Mendelian theory of independent segregation of discrete units.[4]

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[3] Cook, O. F., "Transmission Inheritance Distinct from Expression Inheritance," *Science*, N. S., 25: 911, 1907.

[4] Examples of coherence of characters in cotton hybrids have been de-

Mendelian reactions are likely to be obtained when defective mutations, such as cluster cottons or hornless breeds of cattle, are crossed with normal varieties, but not when normal representatives of two species are crossed, like the Upland and Egyptian cotton or the cow and the zebu. Though there can be no question of the purity of the parental stocks with reference to many contrasted characters, interspecific hybrids seldom show the typical Mendelian behavior.

NON-MENDELIAN BEHAVIOR OF THE BOVINE HYBRIDS

The facts stated by Dr. Nabours regarding the bovine hybrids do not show that the behavior of the characters is essentially Mendelian. Even if the parental breeds were segregated in the same proportions as in simple Mendelian hybrids, the result would still be essentially non-Mendelian, for the parental types differ by many sharply contrasted characters. Such a segregation of "pure Brahma and pure Durham" would mean that there had been a complete coherence of all of the characters of the two parental stocks, instead of a Mendelian segregation and recombination of independent units. The actual facts appear to lie somewhere between complete coherence and complete segregation.

If the Mendelian conceptions of heredity applied to these bovine hybrids, the segregation of "pure Brahma and pure Durham," instead of appearing to be the rule, would occur only in extremely rare cases, because of the numerous differences of the parental types. Indeed, my own impression on this point is somewhat more Mendelian than the account given by Dr. Nabours. Though it was noticed that several individuals of the second generation were distinctly more Brahma-like and more Durham-like than any of the first generation, there were only two or three that suggested the idea of complete segregation of the parental types. The fact that impressed me was not that so much segregation of the contrasted parental characters had taken place in the second generation, but so little. The various colors and textures of hair and skin, the horns, humps and dewlaps were generally brought into coordinated, harmonious expression,

scribed in several publications of the Bureau of Plant Industry, U. S. Department of Agriculture. Bull. 147, "Suppressed and Intensified Characters in Cotton Hybrids"; Bull. 156, "A Study of Diversity in Egyptian Cotton," and Cir. 66, "Cotton Selection on the Farm by the Characters of the Stalks, Leaves and Bolls."

instead of behaving as separate "units" combined by indiscriminate alternative transmission. Even the more complete reversions to the parental types may be considered as results of non-Mendelian coherence of characters in expression, rather than as examples of Mendelian segregation and recombination of independent "units."[5]

COMPARISON OF BOVINE HYBRIDS WITH COTTON HYBRIDS

The practical question to be determined is whether the Durham-like and Brahma-like individuals of the second and later generations are equal to the original parental varieties, and whether the intermediate individuals maintain the average of the first generation. In the second generation of interspecific cotton hybrids it is usual to find many degenerate plants with an obvious resemblance to one or the other of the parental stocks, though usually abnormal and inferior. But among the cattle the second generation hybrids seemed much less different from the first generation, both in constitution and in external features. No general tendency to inferiority in the second generation, as compared with the first, either in vigor or in resistance to ticks, had been detected by Mr. Borden. But the experiments have not continued long enough to afford adequate evidence on this point.

If the analogy of cotton should be found to apply with the bovine hybrids the Brahma-like and Durham-like animals that appear in the second and later generations will not prove to be equal to the Brahmas and Durhams that have not been hybridized, nor will the intermediate individuals show as high an average as the first generation. One of the usual results of crossing, even among varieties of the same species, is to destroy the effects of previous selection in establishing a uniform expression of the characters of the parent varieties. The fact that many of the second generation of Brahma hybrids are magnificent animals does not prove that equally superior hybrid varieties can be established. To increase the pure stock of Brahma cattle, and thus increase the possibilities of producing first generation hybrids, may be more important than the breeding of hybrid varieties. At least this is the suggestion to be drawn from the failure of many attempts to develop superior useful varieties of cotton and other seed-propagated plants from interspecific hybrids. As a barrier to a permanent union of two species degeneration in the second or later generations of a hybrid stock may be as effective as sterility in the first generation. It may prove very fortunate that Mr. Borden has imported Brahma cows as well as bulls, for this may make it possible to perpetuate the Indian breeds in Texas.

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[5] In a more recent paper Dr. Nabours has recognized the divergence from typical Mendelism, in the following statement: "As a matter of fact, observations made this summer and to be described later, indicate that the segregation is not so simple as it at first appeared to be." See, "Possibilities of a New Breed of Cattle for the South", in American Breeders Magazine, **4**: 45, March, 1913.

A tendency to deterioration in the later generations of hybrids is likely to be masked as long as hybrids are crossed back on one of the parental stocks, instead of being bred with each other. This is because even dilute hybrids share some of the stimulation effect shown in the first generation. But these questions of vigor and fertility, though of fundamental importance in practical breeding, lie outside of the range of the Mendelian theory. Vigor and fertility are phenomena of expression in the first generation, whereas the theory of Mendelism relates to the transmission of characters to the second and later generations. Mendelism has served a useful purpose in opening the way to a better understanding of the various forms of alternative inheritance, but the overshadowing Mendelian theory of heredity as a process of alternative transmission of character-unit particles needs to be cleared away.

This theory that alternative inheritance is due to alternative transmission does not lead to more correct ideas of the nature of heredity or to better methods of breeding. Instead of providing us with a simple method of making any desired combination of characters of different species, as writers on Mendelism have led the public to believe, the facts of alternative inheritance indicate that it is very difficult, if not altogether impossible, to secure permanent combinations of characters of different species. In plants that can be propagated from cuttings, hybrid combinations can be maintained, but this affords no assurance regarding types that are limited to sexual reproduction.

O. F. Cook

Bureau of Plant Industry,
U. S. Department of Agriculture,
December 27, 1912